



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2019

Toddlers show sensorimotor activity during auditory verb processing

Antognini, Katharina ; Daum, Moritz M

Abstract: Language that describes actions, for instance verbs, can help to predict future actions of conspecifics in social interactions. Language and action are therefore interrelated. This interrelation has been described on a behavioral level for adults and toddlers. Furthermore, in adults, the sensorimotor system is involved in this interrelation. However, little is known about the early interrelation on the neural level at the onset of verb acquisition. In the present study, we examined the role of the sensorimotor system during the processing of acoustically presented verbs that describe dynamic actions and visually presented actions in toddlers, who are in the earliest stage of expressive language development. The activity of the sensorimotor system, in particular the suppression of the mu rhythm, was measured by means of electroencephalography (EEG). Results showed a significant suppression of the mu rhythm during both the processing of action verbs and observed actions, but not during the processing of pseudoverbs. This suggests that the sensorimotor system is already involved in the processing of action and language early in life.

DOI: <https://doi.org/10.1016/j.neuropsychologia.2017.07.022>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-138908>

Journal Article

Accepted Version



The following work is licensed under a Creative Commons: Attribution-NonCommercial-NoDerivatives 4.0 International (CC BY-NC-ND 4.0) License.

Originally published at:

Antognini, Katharina; Daum, Moritz M (2019). Toddlers show sensorimotor activity during auditory verb processing. *Neuropsychologia*, 126:82-91.

DOI: <https://doi.org/10.1016/j.neuropsychologia.2017.07.022>

Manuscript accepted for publication in Neuropsychologia

Toddlers show sensorimotor activity during auditory verb processing

Katharina Antognini^a and Moritz M. Daum^a

^a Department of Psychology, University of Zurich, Switzerland

Correspondence concerning this article should be addressed to:

Katharina Antognini

University of Zurich

Department of Psychology

Developmental Psychology: Infancy and Childhood

Binzmuehlestrasse 14, Box 21

8050 Zurich

Switzerland

Email: k.antognini@psychologie.uzh.ch

Abstract

Language that describes actions, for instance verbs, can help to predict future actions of conspecifics in social interactions. Language and action are therefore interrelated. This interrelation has been described on a behavioral level for adults and toddlers. Furthermore, in adults, the sensorimotor system is involved in this interrelation. However, little is known about the early interrelation on the neural level at the onset of verb acquisition. In the present study, we examined the role of the sensorimotor system during the processing of acoustically presented verbs that describe dynamic actions and visually presented actions in toddlers, who are in the earliest stage of expressive language development. The activity of the sensorimotor system, in particular the suppression of the mu rhythm, was measured by means of electroencephalography (EEG). Results showed a significant suppression of the mu rhythm during both the processing of action verbs and observed actions, but not during the processing of pseudoverbs. This suggests that the sensorimotor system is already involved in the processing of action and language early in life.

Key words: Language; Action Perception; Embodiment; Mu Rhythm; Mirror Neuron System; Development

1. Introduction

Language, and more specifically verbs, are an inherent part of social interactions (Tomasello, 2001). In social interactions, verbs can serve as cues to predict future behavior, especially future actions of conspecifics (Springer, Huttenlocher, & Prinz, 2012). It has been demonstrated that action processing and verb processing are interrelated in adults (Fischer & Zwaan, 2008; Pulvermüller, 2005; Springer et al., 2012) and toddlers (Gampe & Daum, 2014; Gampe, Brauer, & Daum, 2016). In adults, extensive literature shows that the sensorimotor system is involved in this interrelation (Buccino et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; Mollo, Pulvermüller, & Hauk, 2016; Moreno, de Vega, & León, 2013; Rüschemeyer, Brass, & Friederici, 2007; van Elk, van Schie, Zwaan, & Bekkering, 2010), resulting in similar brain activations during the production and the visual observation of actions, as well as during listening to action-related verbs. However, it is less well studied how this interrelation develops, and which neural systems are involved. The aim of the present study was to investigate whether sensorimotor involvement in both action and verb processing is already established in toddlers, who are at the beginning of verb acquisition. This study is an important first step towards increasing our understanding of the early interrelation between action and language, since it investigates whether the sensorimotor system underlies the processing of different modalities (linguistic and visual) of action representations, as has been reported in adults already (Pulvermüller, 2005). This means that we study the interrelation of action and language in light of a common neural processing system for different action representations. In the following, we briefly introduce the importance of studying the interplay between language and action from a general, and in particular, from an ontogenetic perspective, focusing on the development of this interplay with a focus on verb acquisition in early childhood. Furthermore, we highlight the commonalities of action and verb processing on a neural level.

Verbs belong to a lexical category that reflects activities, processes, and relations, and as such they are distinct from nouns, which describe entities (Baker, 2003; Golinkoff & Hirsh-Pasek, 2006; Tomasello, 1992). These processes and relations can be concrete and dynamic (e.g., running, grasping), static (e.g., standing, waiting), or abstract (e.g., existing, thinking). In the following we focus on dynamic action verbs, since toddlers' first-acquired verbs are to a great extent verbs that describe observable actions of people, such as drawing and stacking (Golinkoff & Hirsh-Pasek, 2006; Sootsman Buresh, Woodward, & Brune, 2006). Abstract verbs are not acquired until later on (Kauschke, 2012). In addition, for reasons of brevity, when writing *verbs* we refer to these dynamic action verbs. Consequently, we consider early-acquired verbs as a linguistic form of action representations, and as such junctions in which actions and words come together (Golinkoff & Hirsh-Pasek, 2006).

Since verbs and actions are semantically related, and verb acquisition consists of mapping words onto actions (Gentner & Boroditsky, 2001), it seems feasible that verb acquisition does not reflect a process whose development is isolated in the language domain, but is rather closely related to development in the action domain. For instance, one needs to understand an action and its facets to learn the label that maps onto the action (Sootsman Buresh et al., 2006). Therefore, verb acquisition builds on a range of action perception skills, such as the processing of motion, action goals, or intentions (Pulverman, Hirsh-Pasek, Golinkoff, Pruden, & Salkind, 2006). These action perception skills are acquired early on in development, at a prelinguistic stage. For example, the detection of biological motion and the preference for it is an intrinsic ability already present in newborns (Simion, Regolin, & Bulf, 2008). From about 6 months of age, infants perceive actions as being directed towards goals (Biro & Leslie, 2007; Daum, Prinz, & Aschersleben, 2008, 2009; Luo & Johnson, 2009; Woodward, 1998). Furthermore, perceiving actions and their goals is already associated with activity in the sensorimotor system of the brain from a very young age. It has been reported that infants from

the age of 8 months show activity in the sensorimotor system during the observation of someone else's actions (e.g., Marshall, Young, & Meltzoff, 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate, Johnson, Osborne, & Csibra, 2009; Warreyn et al., 2013). The sensorimotor system is thus involved in action perception, which is a basis for verb acquisition (Pulverman et al., 2006).

Later on in development, these early action-perception skills serve to map words onto perceived actions, and in turn to acquire verbs (Sootsman Buresh et al., 2006). Verb comprehension starts at the beginning of the second year of life (Golinkoff & Hirsh-Pasek, 2008) and precedes verb production, which increases at around 18-24 months of age (Kauschke, 2012; Rothweiler & Kauschke, 2007). Furthermore, toddlers reach a total vocabulary of approximately 100 words at this stage (Bates et al., 1994). So an increase in expressive verb vocabulary is not only associated with an increase in age but also with an increase in general language repertoire, i.e. overall vocabulary (Kauschke, 2012).

In adults, who are highly proficient in using verbs, not only temporal and inferior frontal language-processing areas are involved in verb processing, but also the sensorimotor system (Buccino et al., 2005; Hauk et al., 2004; Moreno et al., 2013; Repetto, Colombo, Cipresso, & Riva, 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). However, the sensorimotor system is only involved in verb processing if verbs map closely onto actions, which is the case for action verbs, but not for abstract verbs or pseudoverbs (Buccino et al., 2005; Fargier et al., 2012; Hauk et al., 2004; Moreno et al., 2013; Repetto et al., 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). Abstract verbs describe mental states and processes (e.g., thinking, doubting, believing; Moreno et al., 2013), whereas pseudoverbs are novel and have no semantic content (Fargier et al., 2012). Both stand in contrast to action verbs, which describe movements of body parts. Furthermore, the sensorimotor system processes action

verbs similarly to observed actions (Moreno et al., 2013). This indicates that the sensorimotor system processes different action representations from the action and the language domain. In addition, similar findings have also been reported for the processing of action-related sounds (Kohler et al., 2002; McGarry, Russo, Schalles, & Pineda, 2012; Pineda et al., 2013). Short-term training of pseudoverb-action associations can also induce the sensorimotor mapping of a novel verb onto an unfamiliar action (Fargier et al., 2012). This indicates that, in adults, sensorimotor processing of verbs can result from associative learning (Cooper, Cook, Dickinson, & Heyes, 2013; Heyes, 2010). Verbs that have been mapped onto actions, either by short-term training or life-long experience with language, are thus associated with sensorimotor activity in adults. In this study, we investigated whether this also holds true for toddlers who are at the beginning of this mapping process. Adults have an immense repertoire of verbs and actions at their disposal which is based on their lifetime experience with both language and actions. In contrast, early in life, children are in the process of acquiring proficiency in both language and action. The question is, therefore, under which circumstances (e.g., motor skills, language status) the sensorimotor system starts to become involved in the processing of different action representations, such as observed actions, action sounds, or action verbs in early development.

Similar to the associative learning reported in the context of pseudoverbs in adults (Fargier et al., 2012), associative learning can result in sensorimotor processing of action-related sounds in 7- to 9-month-olds, who displayed activity in sensorimotor brain regions for sounds that had been associated with shaking actions in a training phase (Gerson, Bekkering, & Hunnius, 2015; Paulus, Hunnius, & Bekkering, 2013; Paulus, Hunnius, van Elk, & Bekkering, 2012). It was postulated that sensorimotor activity in response to sounds is the result of an association between the shaking action and the effect of the shaking (Gerson et al., 2015; Paulus et al., 2012). If this association becomes strong enough, the perception of the action effect triggers

1 sensorimotor activity (Cooper et al., 2013; Heyes, 2010). These findings provide evidence for
 2 the assumption that associative learning already plays a role in the sensorimotor processing of
 3 different action representations early on in development (Gerson et al., 2015; Paulus et al.,
 4 2013, 2012). Additionally, first-hand experience with actions influences the strength of
 5 association between different action representations (Locatelli, Gatti, & Tettamanti, 2012).
 6 For instance, action sounds were associated with stronger sensorimotor activity when they
 7 were linked to actually produced actions than to merely observed actions (Gerson et al.,
 8 2015). Also, sensorimotor activity in response to observed actions is stronger when the infant
 9 is able to perform the action (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008; Yoo,
 10 Cannon, Thorpe, & Fox, 2016). This effect could be explained with the potential strength of
 11 the representations of an action. Representational strength is a concept within the account of
 12 graded representations, where strength depends on experience with a given entity that is
 13 represented (Munakata, McClelland, Johnson, & Siegler, 1997). Furthermore, strong
 14 representations provide clean neural signals that allow connections to other representations in
 15 the cognitive system: For instance, strong motor representations of an action allow
 16 connections with auditory representations of an action (i.e., sound that is elicited by
 17 performing the action). On a neural level, the graded representations account states that
 18 representational strength could be operationalized by neuronal firing rates, firing coherence,
 19 and connectivity (Munakata, 2001). Previous research showed that experience influences
 20 representational strength, for example of objects; that is, object representations are stronger if
 21 infants are more experienced in perception of and interaction with the objects (Shinsky &
 22 Munakata, 2005). Furthermore, representational strength increases with age, which can again
 23 be explained by extended experience with increasing age (Munakata, 2001). At the age of 22
 24 months, toddlers retrieve and update representations more easily than at 19 months (Ganea,
 25 Shutts, Spelke, & DeLoache, 2007). For the present study, we assume a similar association
 26 between experience, representational strength, and sensorimotor involvement for linguistic

action representation as has been reported for visual action representation. Consequently, we expect the sensorimotor response to verbs to be stronger for verbs that a toddler is able to vocalize in contrast to verbs that are either only part of the toddler's receptive vocabulary or that are unknown, such as pseudoverbs. Similar to the retrieval of object representations from memory (Ganea & Saylor, 2013), the retrieval of the meaning of a verb from memory will then be better for verbs that are more strongly represented. This means that sensorimotor involvement in verb processing could be associated with proficiency or experience in using verbs.

As mentioned above, adults, who are proficient verb users, show sensorimotor involvement in verb processing (Buccino et al., 2005; Hauk et al., 2004; Moreno et al., 2013; Repetto et al., 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). In addition, a functional magnetic resonance imaging study already showed sensorimotor processing for auditorily presented action verbs in preschoolers (4-5 years old), who have a smaller expressive verb repertoire than adults (James & Maouene, 2009).¹ More specifically, the preschoolers' sensorimotor system showed somatotopically distributed activity corresponding to the effector limbs used to perform the action described by the verb (James & Maouene, 2009). Similar somatotopic activation patterns are reported in studies with adult participants (Pulvermüller, 2005). However, 4- to 5-year-olds still have already well-developed action and verb repertoires, which are smaller, but far closer to the adult repertoires than to those of toddlers, especially with respect to the simple actions and action verbs used in the studies. It therefore remains unclear whether the sensorimotor system also plays a role in the processing of verbs in early stages of verb acquisition.

¹ The modality of stimulus presentation was different from studies in adults, which mostly use visual presentation of verbs (e.g., Hauk, Johnsrude, & Pulvermüller, 2004; Moreno, de Vega, & León, 2013).

NEURAL INTERRELATION OF ACTION AND LANGUAGE IN TODDLERS

We investigated this question by examining sensorimotor activity during action-verb processing in 18- and 24-month-olds. We assumed that toddlers in both age groups have already acquired some basic receptive action-verb repertoire (Golinkoff & Hirsh-Pasek, 2008), but still differ in their expressive action-verb repertoire (Bates et al., 1994). We acoustically presented sentences with early-acquired action verbs and pseudoverbs, and showed video clips of means-end actions. Pseudoverbs are an ideal control condition for two reasons. First, in adults, pseudoverbs were not associated with sensorimotor activity (Fargier et al., 2012). Second, unlike abstract verbs, pseudoverbs do not carry semantic information but have still a valid phonotactic structure in contrast to non-words (Friedrich & Friederici, 2005). During stimulus presentation, the toddlers' sensorimotor activity was assessed by means of electroencephalography (EEG). Early-acquired action verbs were defined according to normative data as verbs that, on average, are in the expressive verb repertoire of 15 % of 18-month-olds and 60 % of 24-month-olds (Szagun, Stumper, & Schramm, 2009). Sensorimotor activity was measured by suppression of the mu rhythm, which is within the alpha range and is typically present over central electrode sites (Hobson & Bishop, 2016; Marshall & Meltzoff, 2011). The mu rhythm is strongly present in the EEG signal when the sensorimotor system is at rest, but gets suppressed when the system is activated (e.g., during action production or perception; Cuevas, Cannon, Yoo, & Fox, 2014). In infants, the frequency band of interest is 6-9 Hz (Marshall, Bar-Haim, & Fox, 2002; Stroganova, Orekhova, & Posikera, 1999), which is lower than in adults (8-13 Hz; Marshall & Meltzoff, 2011). Studies report a gradual increase in the peak frequency with increasing age. It has been reported that the peak frequency is about 8 Hz at 24 months of age (Berchicci et al., 2011; Marshall et al., 2002). Despite this difference in the frequency range, the function and topography of the mu rhythm are similar in infants, toddlers, and adults (Marshall & Meltzoff, 2011).

NEURAL INTERRELATION OF ACTION AND LANGUAGE IN TODDLERS

The following three main questions guided the present research: First, do toddlers show a suppression of the mu rhythm when listening to action verbs similar to the reported suppression when observing actions (Warreyn et al., 2013)? We expected this to be the case, since toddlers already have a receptive vocabulary of action verbs (Golinkoff & Hirsh-Pasek, 2008) as verified by a parent questionnaire, and therefore associations between actions and verbs are established. Second, is the suppression of the mu rhythm different in response to action verbs than to pseudoverbs? The adult sensorimotor system responds to pseudoverbs only after associations with actions have been formed by training (Fargier et al., 2012). However, it remains an empirical question whether pseudoverbs are associated with sensorimotor activity or not in toddlers. One possibility is that pseudoverbs are recognized as verbs describing an (as yet unlabeled) action due to their morphology, and are therefore processed similarly to action verbs that are already in the child's vocabulary (Hernandez Jarvis, Merriman, Barnett, Hanba, & van Haitsma, 2004; Mani, Durrant, & Floccia, 2012). Another possibility is that pseudoverbs are not associated with sensorimotor activity in toddlers, since the pseudoverbs do not map onto actions, which would parallel findings from a study in adults (Fargier et al., 2012). Third, is the suppression of the mu rhythm in response to verbs different for 18- and 24-month-olds? Within this age range, toddlers differ with respect to expressive verb repertoire (Bates et al., 1994), which might affect sensorimotor activity in response to verbs depending on age. There is evidence that greater expressive vocabulary was associated with implicit production of nouns that fit a preceding verb (Mani, Daum, & Huettig, 2016; Mani & Huettig, 2012). It is a feasible assumption that this task includes mental simulation of the action described by the verb, which facilitates the prediction of the appropriate noun or object. If a greater expressive verb vocabulary – and in turn more experience with verbs and hence stronger verb representations (Munakata, 2001; Shinsky & Munakata, 2005) – is associated with better mental simulation of the action, we could assume that the suppression of the mu rhythm is stronger for toddlers with a larger expressive verb

vocabulary. This is because the suppression of the mu rhythm is related to mental simulation of actions (Jeon, Nam, Kim, & Whang, 2011; Nam, Jeon, Kim, Lee, & Park, 2011; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Pineda, Allison, & Vankov, 2000). However, the strength of the sensorimotor verb-action association could depend rather on motor experience with the action than verb repertoire. We know that motor experience is essential to form associations between actions and action effects (Gerson et al., 2015). Accordingly, it is plausible to hypothesize that motor experience is beneficial for the formation of an association between the action and the corresponding verb. However, we assume that both age groups have similar motor experience with the particular actions that were presented to the children in the present study. This implies that the two age groups are not expected to differ with respect to the suppression of the mu rhythm in response to action verbs.

2. Materials and Methods

2.1 Participants

We included 20 toddlers (7 female) aged 18 months ($M = 566.6$ days, range = 551-579 days) and 27 toddlers (15 female) aged 24 months ($M = 747.2$ days, range = 724-777 days) in the final sample. All toddlers provided a minimum of six trials per condition and completed at least the first block of the procedure (verb block). This sample was used for the analysis involving the first block. In total, an additional 28 toddlers aged 18 months and 20 toddlers aged 24 months were tested but excluded due to technical problems ($n = 1$), refusal to keep the net on their head ($n = 5$), or because they did not provide enough artifact-free trials ($n = 42$). The average attrition rate of 50.5% was within the expected range for this age group (DeBoer, Scott, & Nelson, 2013) and comparable to other studies in the field (Bache et al., 2015; Reid, Striano, & Iacoboni, 2011; Stapel, Hunnius, van Elk, & Bekkering, 2010; Warreyn et al., 2013). To compare the neural response to verbs and observed actions, we

selected a subsample of toddlers ($n = 33$) who completed both blocks of the procedure (verb block and observation block), satisfying the criterion of a minimum of six trials per condition in both blocks. This subsample consisted of 14 18-month-olds (4 female) and 19 24-month-olds (10 female).

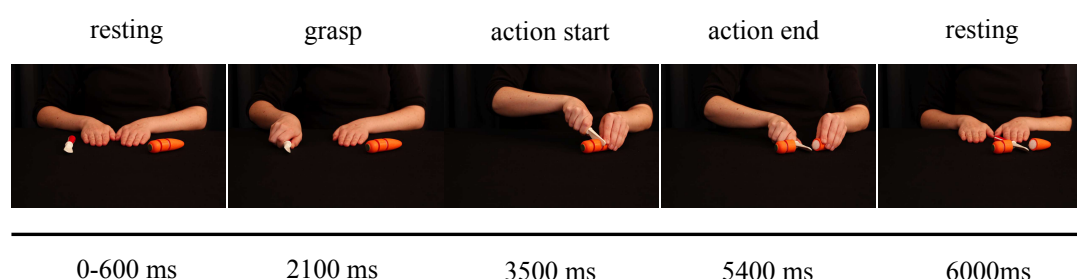
All toddlers were recruited from local birth records. They were born full term (week of gestation ≥ 37), had normal birth weight (≥ 2500 g), grew up in Swiss-German monolingual households and had right-handed parents. The study was approved by the local ethics committee. Caregivers gave written informed consent. The toddlers received a small age-appropriate toy (value equivalent to 5 USD) and a printed certificate for their participation in the study.

2.2 Stimuli

We used three types of materials: auditory stimuli, visual stimuli, and play material. The auditory stimuli consisted of six sentences spoken by a native Swiss-German female speaker. The full duration of each sentence was 1100 ms. The sentence structure was as follows: “Ich” [I] from 0-400 ms and a verb (action verb or pseudoverb) from 500-1100 ms after sentence onset. We used three different familiar action verbs: “maale” [to draw], “schiide” [to cut], “baue” [to build]. These had been chosen because they were classified as early-acquired verbs according to the Swiss-German adaptation the language questionnaire FRAKIS (Szagun et al., 2009). The corresponding pseudoverbs were constructed such that they had the same initial sound and end sound as the familiar action verb: “mieke“, “schraade“, “bope”.

The visual stimuli consisted of video clips depicting means-end actions that corresponded to the familiar action verbs used in the auditory stimuli. The video clip showed an actress’s

1 arms, hands, and torso from a third-person perspective. The actress sat at a table with two
 2 objects lying in front of her. The object near her right hand (i.e., on the left side of the screen)
 3 was always the means object (e.g., green pencil, plastic toy knife, blue wooden building
 4 block), whereas the object near her left hand (i.e., on the right side of the screen) was the goal
 5 object (e.g., yellow piece of paper, orange toy carrot with three pieces held together by
 6 Velcro, two stacked yellow and red wooden building blocks). The structure of the actions was
 7 as follows (see Fig. 1): The actress sits at the table with her hands in a resting position (0-
 8 600 ms). Then, she lifts her right hand and grasps the means object (2100 ms), which is
 9 transported towards the goal object. On arrival at the goal object (3500 ms), she performs the
 10 appropriate action. After finishing the action (5400 ms), she puts the means object down and
 11 returns her hands to the resting position. All these steps taken together resulted in a 6000 ms
 12 video clip. As play material, we used the same objects as shown in the video clips of the
 13 means-end actions.



14
 15 **Fig. 1.** Structure of the video clips. Here, the action *to cut* is depicted with respect to the
 16 action boundaries resting, grasping and action execution. The structure of the other actions
 17 was analogous.

18

19 2.3 Procedure

20 On arrival at the lab and as part of the standard procedure, the caregivers were asked to
 21 provide information about years of education and handedness of both parents. Furthermore, to

NEURAL INTERRELATION OF ACTION AND LANGUAGE IN TODDLERS

1 assess action-verb production, the caregivers were asked to indicate whether the toddler
2 understood and spontaneously produced (i.e., vocalized) the action verbs that were presented
3 in the EEG paradigm. Verb comprehension was not assessed directly, since parent reports
4 have poor validity, especially for the second year of life (Eriksson, Westerlund, & Berglund,
5 2002; Feldman et al., 2005; Tomasello & Mervis, 1994). Language status was not assessed
6 otherwise. Moreover, caregivers were asked to indicate whether the toddler performed the
7 actions that we used in the EEG paradigm in their daily lives or during playtime.

8
9 The EEG paradigm took place in a dimly lit, electrically shielded and sound-attenuated room.
10 The toddler sat on the caregiver's lap, at an approximate distance of 60 cm from a 17-inch
11 computer screen with adjacent loudspeakers. We used the software Presentation 18.1
12 (Neurobehavioral Systems, USA) to present the auditory and visual stimuli. The EEG
13 paradigm consisted of two separate blocks, which were always kept in the same order. The
14 verb block came first, followed by the observation block. The order was kept constant to
15 exclude any possible carry-over effects from action observation onto verb processing.

16
17 In the verb block, the trials were presented in random order, with a maximum of three trials of
18 the same condition (action verb, pseudoverb) in a row. Throughout the sentence presentation,
19 a red dot with a diameter of about 3 cm was presented in the middle of the screen. In addition,
20 this dot served as a fixation point in the between-stimulus interval (BSI), which had a
21 duration of 2000 ms. During the sentence presentation as well as the BSI, the dot changed its
22 color gradually from red to yellow and back to red. The gradual color change was chosen to
23 keep the toddlers' quiet attention using a changing stimulus (Cuevas et al., 2014) that is not
24 associated with an action, since there was no translational movement or contingency with any
25 other stimulus. We suppose that the gradual color change is therefore not interpreted as
26 action. After every third trial, or if the toddler became inattentive, an attention grabber was

presented. Attention grabbers consisted of a video depicting a spiraling screensaver with a jingling sound. The verb block consisted of a maximum of 60 trials (30 trials per condition), but was terminated by the experimenter if the toddler was not attending to the stimuli anymore (i.e., inattention for more than 6 trials in a row).

The observation block was divided into three sub-blocks with respect to the three actions that were used as action verbs in the verb block. The order in which the sub-blocks were presented was randomized. For each action, the video clip was presented six times in a row. The BSI in the observation block was identical to the BSI in the verb block in terms of the stimulus shown and the timing. After these six identical video clips, the experimenter handed the toddler the play material that the actress had used in the video clip. By saying “It’s your turn!”, the experimenter prompted the toddler to imitate the action shown in the video clip. The imitation trial ended after the toddler had completed the action, or if the toddler did not initiate the action after 15 seconds.

The imitation trials were used to maintain the toddlers’ attention, but EEG was not further analyzed.² Because of these imitation trials the aforementioned subdivision into sub-blocks was necessary in order to avoid carry-over effects from the imitation of an action onto the observation of the action.

2.4 EEG recording and analysis

The EEG was recorded with a NetAmps 300 amplifier (Electrical Geodesics Inc., Eugene, OR, USA) at 500 Hz sampling rate and a 128-channel sensor net with infant layout (Electrical

² Initially, we intended to analyze the EEG data from the imitation condition to have a measure for action execution (Cuevas, Cannon, Yoo, & Fox, 2014). However, we did not obtain enough trials for the analysis because of very strong movement artifacts, mostly due to head movements and because toddlers refused to interact with the play material.

Geodesics Inc., Eugene, OR, USA). During recording, an online 0.1 Hz high-pass filter was applied and data were referenced to the vertex. Impedances were kept below 50 k Ω . After EEG acquisition, the data were preprocessed in the EEGLAB toolbox (Delorme & Makeig, 2004). We applied a 0.3-30 Hz band-pass filter and removed the outermost channels (due to insufficient contact with the scalp; Filippi et al., 2016; Nyström et al., 2011). Trials in which the toddler moved or did not attend to the stimuli were removed. In the verb block, on average 51% of the epochs from the action-verb condition and 48 % of the epochs from the pseudoverb condition were removed. In the observation block, on average 43 % of the epochs were removed. We performed an independent component analysis (ICA) to identify and remove artifacts due to eye movements, sweating, and heartbeat (Delorme & Makeig, 2004). Finally, we interpolated missing channels using spherical interpolation and re-referenced the data to common average reference.

Data from the verb block were segmented according to condition (action verb, pseudoverb). We extracted 2500 ms epochs, consisting of 1000 ms before sentence onset and 1500 ms after sentence onset. On average, we obtained 12.5 trials for the action-verb condition (range = 6-24) and 12.7 trials for the pseudoverb condition (range = 6-26). Data from the observation block were segmented into 8000 ms epochs with a 1500 ms period before and a 6500 ms period after video onset. We obtained an average of 9.6 trials for the action-observation condition (range = 6-16).

Data were analyzed in Matlab (R2014b) by performing a time-frequency analysis over a frequency range between 4 and 20 Hz using Morlet wavelets with constant 5 cycles and windowed with a cosine square window. The analysis provided raw power values [μV^2] that were then averaged over trials. We calculated the mean power over a frequency band between 6-10 Hz. This frequency band was chosen because at 24 months of age the peak frequency

has been reported to be at about 8 Hz (Berchicci et al., 2011; Marshall et al., 2002). We chose a frequency band with ± 2 Hz around this peak frequency. Extracting individual frequency bands from the imitation trials, as suggested in the literature (Cuevas et al., 2014), was not possible because most imitation trials were highly contaminated with movement artifacts and many toddlers refused to interact with the play material. Furthermore, two time windows were selected, for which the average power was calculated over the time domain. For the epochs of the verb block, the first time window (baseline) represented the 0-400 ms period, where the “Ich” [I] had been presented. This baseline was chosen because it includes the same visual stimulation (color-changing dot) and auditory information that is not, however, a verb. This is to account for possible effects of hearing any type of vocalization on sensorimotor activity. The second time window represented the full verb period between 500-1100 ms. For the epochs from the observation block, we selected the first time window between -1000-0 ms (baseline), which represents the second half of the BSI. We chose only the second half of the BSI to exclude any carry-over effects from the trial before. A second time window considered the whole length of the video clip (0-6000 ms)³.

Since we expected differences in activity over central sites, we selected two clusters of channels, which correspond to C3 and C4 in the 10-20 system (left central: E29, E30, E35, E36, E37, E41, E42; right central: E87, E93, E103, E104, E105, E110, E111). Furthermore, we selected an occipital cluster (E66, E69, E70, E74, E75, E76, E79, E82, E83, E84, E89) to show the specificity of our hypothesized effect to the central sites. The averaged raw power values [μV^2] were used to calculate event-related desynchronization (ERD) values according to Pfurtscheller (2001). We used the first time window in each of the conditions as the

³ Additionally, we selected a time window from 3500-5400 ms, which represents the period of time where the actress acts on the goal object. There was no difference between this time window and the full time window (grasping and action on goal object) with respect to sensorimotor activity, $F(1,31) = 1.78$, $p = .191$. Therefore, we did not further analyze this shorter time window, but instead the full video clip we presented.

baseline period and the second time window as the activation period. Statistical analyses were performed with the R statistical package (R Core Team, 2016).

3. Results

3.1 Questionnaire Data

We analyzed the language questionnaire data for all $n = 47$ toddlers in the final sample. A two-sample t-test for differences between the age groups in the expressive vocabulary regarding the words we used in the EEG paradigm indicated that the 24-month-olds produced (i.e., vocalized) the verbs significantly more often than the 18-month-olds, $t(45) = -8.91$, $p < .001$. Furthermore, we ran a two-sample t-test to analyze differences in action production of the actions that were used in the video clips during the EEG paradigm. Results indicated that there was no difference in action production between the two age groups, $t(45) = -0.957$, $p = .344$.

3.2 EEG Data

Firstly, we conducted an analysis for the verb block including all subjects with a minimum of 6 artifact-free trials per condition (action verb, pseudoverb). Secondly, we compared ERD between action verbs and action observation for those toddlers who provided a minimum of six trials per condition in both blocks (verb block, observation block). We chose this subsample because all toddlers have completed the verb block before the observation block. Thus, exposure to the corresponding action verbs was the same for this group of toddlers, which would not have been the case if we had chosen all toddlers who completed the observation block irrespective of the verb block.

3.2.1 Verb block

To answer our second question of whether action verbs and pseudoverbs differ in their involvement of the sensorimotor system, we ran a mixed-effects analysis of variance

1 (ANOVA) on mean ERD values. The within-subject factors were condition (action verb,
 2 pseudoverb) and cluster (left central, right central, occipital). The between-subjects factor was
 3 age group (18 months, 24 months). This analysis revealed a significant main effect of cluster,
 4 $F(2, 90) = 4.66, p = .012, \eta_p^2 = 0.022$. No main effects for condition, $F(1, 45) = 1.40,$
 5 $p = .243$, or age group, $F(1, 45) = 0.210, p = .811$, were found. Further, results revealed an
 6 interaction effect between cluster and condition, $F(2, 90) = 3.26, p = .043, \eta_p^2 = 0.010$. No
 7 other interaction effects reached significance (all $p > .548$). To further analyze the interaction
 8 effect between cluster and condition, we conducted paired t-tests which indicated that ERD
 9 for action verbs ($M = -5.07, SD = 15.5$) was significantly different from ERD for pseudoverbs
 10 ($M = 4.97, SD = 29.2$) in the left central cluster $t(46) = -2.10, p = .042$ (see Fig.2), but not in
 11 the other clusters (all $p > .668$). Furthermore, one-sample t-tests indicated that ERD for action
 12 verbs was different from zero in the left central ($M = -5.07, SD = 15.5$), $t(46) = -2.24, p = .030$
 13 and in the occipital cluster ($M = -7.41, SD = 14.8$), $t(46) = -3.44, p = .001$, while ERD for
 14 pseudoverbs differed from zero only in the occipital cluster ($M = -6.07, SD = 15.8$), $t(46) = -$
 15 $2.63, p = .011$.

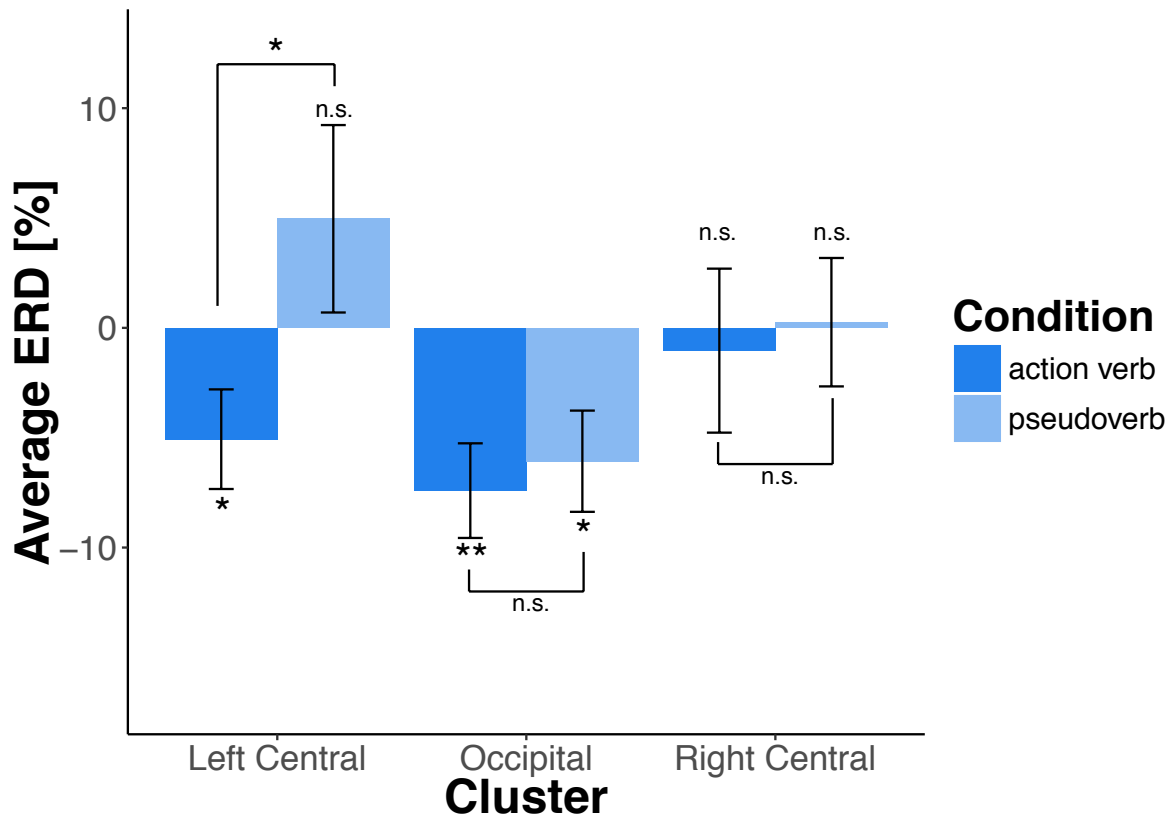


Fig. 2. Average ERD within the toddler mu range of 6-10 Hz for action verbs and pseudoverbs, split by electrode clusters. The ERD indicates % changes with respect to the baseline time window. Error bars indicate ± 1 standard error. Significant differences are indicated by $* = p < .05$, $** = p < .01$. Non-significant values are indicated by n.s.

3.2.2 Verb block compared to observation block

To answer our first question of whether action verbs and observed actions both involve the sensorimotor system, we compared the ERD for action verbs and for action observation in the sample of toddlers ($n = 33$), who completed both blocks satisfying the criterion of a minimum of 6 trials per condition. We ran a mixed-effects ANOVA including the within-subject factors condition (action verb, action observation) and cluster (left central, right central, occipital), and the between-subjects factor age group (18 months, 24 months). With respect to the time window for action observation, we chose the full action period, since it did not differ from the period where the actress acted on the goal object. The results revealed a significant main

effect of cluster, $F(2, 62) = 11.7, p < .001, \eta_p^2 = 0.063$. Furthermore, the results indicated an interaction effect between cluster and condition, $F(2, 62) = 21.9, p < .001, \eta_p^2 = 0.106$, and an interaction effect between age group and cluster, $F(2, 62) = 5.62, p = .006, \eta_p^2 = 0.031$. No other main effects (all $p > .073$) or interaction effects (all $p > .244$) reached significance.

To evaluate whether the conditions differed within the clusters, we ran paired t-tests on each cluster. In the right central cluster, ERD for action verbs ($M = -5.12, SD = 19.1$) was significantly weaker than ERD for action observation ($M = -26.43, SD = 14.4$), $t(32) = 5.26, p < .001$. In the left central and in the occipital cluster, ERD for action verbs and action observation did not differ significantly (all $p > .461$). One-sample t-tests indicated that ERD for action verbs was different from zero in the left central cluster ($M = -7.62, SD = 14.9, t(32) = -2.93, p = .006$) and in the occipital cluster ($M = -9.44, SD = 14.3, t(32) = -3.78, p < .001$). For action observation, one-sample t-tests indicated that ERD differed from zero in the right central ($M = -26.4, SD = 14.4, t(32) = -10.6, p < .001$) and in the occipital cluster ($M = -10.9, SD = 14.5, t(32) = -4.31, p < .001$).

To investigate whether ERD for age groups differed within clusters, and thus to answer our third question, we ran two-sample t-tests within clusters to compare the age groups. The results indicated that the difference between ERD for 18-month-olds ($M = -13.9, SD = 11.2$) and 24-month-olds ($M = -7.40, SD = 7.21$) was marginally significant, $t(31) = -2.02, p = .053$, in the occipital cluster. ERD scores did not differ between age groups in the other clusters (all $p > .095$).

4. Discussion

We investigated the involvement of toddlers' sensorimotor systems during the processing of acoustically presented verbs. Toddlers listened to sentences with phonologically similar

action verbs and pseudoverbs, while the response of the mu rhythm was recorded using EEG. Additionally, to compare the brain responses between acoustically presented verbs and visually presented actions, we also recorded the mu rhythm response to observed actions.

In the following, we discuss the results of the current study with respect to our three main questions: First, do toddlers already show an activation of their sensorimotor system indicated by a suppression of the mu rhythm when listening to action verbs as they do when observing actions? Second, is the suppression of the mu rhythm different in response to action verbs than to pseudoverbs? Third, is the suppression of the mu rhythm in response to verbs different for 18- and 24-month-olds?

4.1. Do toddlers show a suppression of the mu rhythm when listening to action verbs?

We first discuss the results concerning action verbs. Secondly, we discuss the neural responses for observed actions, and thirdly, we consider the similarities of neural responses to action verbs and observed actions.

4.1.1. Action verbs

We found a significant suppression of the mu rhythm over the left central electrode cluster in response to action verbs. However, this neural response was not specific to central sites, since we also found a suppression of the occipital alpha rhythm in response to action verbs. The central effect indicates that the sensorimotor system is active during the processing of action verbs. This effect was lateralized towards the left hemisphere. The lateralization of the mu suppression towards the left hemisphere can be interpreted in two different ways. Firstly, the activity of the sensorimotor system could be left-lateralized because the toddlers mentally simulate performing the action. We presume that our toddlers are right-handed, since we included only toddlers with right-handed parents in the sample and the probability of left-

handedness when having two right-handed parents is very low (McManus & Bryden, 1992). Furthermore, the majority of the population is right-handed. Simulating the performance of an action like cutting with the right hand would fit a left lateralization of the suppression of the mu rhythm (Jeon et al., 2011; Nam et al., 2011; Pfurtscheller et al., 2006; Pineda et al., 2000). Secondly, one might interpret the left lateralization in terms of similarities with language processing. Action verbs are a linguistic form of action representation (Barsalou, 2008) and share some commonalities with general language processing, which is known to be left-lateralized in most right-handers (Knecht et al., 2000). This lateralized pattern for the processing of action verbs which we observed in our study has already been reported in adults (Hauk & Pulvermüller, 2011). It was shown that action verbs that indicate a uni-manual action were processed more strongly in the left central cortex for right- as well as left-handers. The authors argue that these results show that the processing of action verbs is more strongly associated with language lateralization, which is presumed to be mostly left hemispheric in both groups, than with handedness itself. In that study, many uni-manual action verbs were presented but amongst these were also the verbs cutting and drawing, which were also part of our paradigm (Hauk & Pulvermüller, 2011). Since we did not have an explicit measure of handedness or language lateralization, nor include left-handed toddlers, we cannot infer which of the two possible explanations is more likely. Future studies could investigate the role of handedness in action verb processing in toddlers.

An often-mentioned criticism regarding sensorimotor activity in response to action-verb processing concerns vocalization. This means that the sensorimotor activity during action-verb processing could not be associated with the motor-related meaning of the verb, but rather with the activity of the vocal tract and the mouth area of the motor cortex during the vocalization of the verb, independent of its meaning. Three reasons speak against this assumption. Firstly, we used a baseline also containing vocalization for the calculation of the

ERD scores. We chose the baseline specifically to account for possible confounding effects of vocalization. Since ERD for action verbs was significantly different from baseline, a mere effect of vocalization can be excluded. Secondly, we have to specify whether it is necessary that the toddler be able to vocalize the action verb himself in order to show sensorimotor activity due to vocalization. A study on the relation between produced or observed actions and action sounds suggests that first-hand motor experience is a prerequisite for sensorimotor activity that is associated with the action sound (Gerson et al., 2015). This means for our study, that own vocalization skills should be a prerequisite for sensorimotor activity related to action verbs, if vocalization is the key factor that drives sensorimotor activity. In our sample, the two age groups differed in terms of their expressive vocabulary for the three verbs we used. This means that, in our sample, very few 18-month-olds vocalized the verbs we presented, whereas a substantial number of 24-month-olds did. If mu suppression in response to action verbs were merely due to imagined vocalization, we would observe a difference between the age groups, which was not the case. Thirdly, there are to date several studies investigating the somatotopic distribution of sensorimotor activity associated with action verbs. These studies, in adults and preschoolers (Hauk et al., 2004; James & Maouene, 2009), indicate that the activation pattern is associated with the limb one would use to perform the action described by the verb. If the sensorimotor activity associated with action verbs could exclusively be explained by heard and simulated vocalization, we would not expect to see a somatotopic distribution of sensorimotor activity. In fact, the topographies rather correspond to the location of the effector limb on the homunculus than to the location of the mouth area. In summary, our results suggest that the processing of action verbs, thus of linguistic action representations, is associated with sensorimotor involvement.

4.1.2 Action observation

The processing of observed actions, thus visual action representations, is a topic that has received much attention in recent years. Like many other studies on infants and toddlers (Nyström et al., 2011; Southgate et al., 2009; Southgate, Johnson, Karoui, & Csibra, 2010; Warreyn et al., 2013; Yoo et al., 2016), we show that toddlers of 18 and 24 months of age activate their sensorimotor system during the processing of observed actions. More specifically, we found a right-lateralized pattern of activity. Additionally, we found that the observation of means-end actions was associated with occipital activity that was slightly more pronounced in the younger age group (marginal significance). This means that there are two characteristics to discuss: the lateralization of the central activity towards the right hemisphere and the occipital activity that differs between age groups.

First, we assume that the lateralization towards the right hemisphere is associated with the modality of presentation. In our paradigm, we always presented the means object on the left side of the screen. In our video clips, the means object was always grasped ipsilaterally with the right hand. It might be the case that the toddlers mentally performed the action from their own perspective, but still with an ipsilateral grasp. To do so, they would use their left hand, which would in turn lead to a strong right-central response. This assumption is difficult to verify, since there is not much literature that is suitable for comparison. Other studies either did not include hemisphere as a factor in their analysis or they did not specify which hand grasped for the object, and nor where the object was placed (Marshall et al., 2011; Nyström et al., 2011; Warreyn et al., 2013). However, one study provides evidence in favor of our assumption. Southgate and colleagues (2009) used live presentation, where the actress's hand always entered the stage from the right side to grasp for an object on the stage. This study showed a significant suppression of the mu rhythm in the left hemisphere only (Southgate et al., 2009). This means that it could be crucial for the lateralization of mu suppression where in

the visual field the first movement happens. In the case of Southgate et al.'s (2009) study the movement happened in the right visual field, which was associated with left central activity. In analogy, in our study, the first movement happened in the left visual field and was associated with right central activity. Future studies could investigate this matter by including visual field as an experimental factor.

Second, we found very strong occipital alpha suppression associated with action observation that was numerically stronger in the younger age group. Since the literature postulates that mu rhythm suppression requires the independence of occipital alpha suppression (Cuevas et al., 2014; Marshall & Meltzoff, 2011), it is important to discuss this occipital effect we observed. Our findings are in line with a study involving 9- and 12-month-olds that showed very strong occipital effects in response to observed actions, which were also stronger for the younger age group (Yoo et al., 2016). In contrast to our study, the 9- and 12-month-olds showed even stronger occipital activity than central activity. The authors state that the strong occipital effects stem from a high degree of attention allocation, which is even stronger in the 9-month-olds (Yoo et al., 2016). Despite this study mirroring our findings, we are aware of the fact that the neural activity we found is not specific to central sites as stated in literature of best practices regarding studies on the mu rhythm (Cuevas et al., 2014; Hobson & Bishop, 2016; Marshall & Meltzoff, 2011).

4.1.3 Action verbs and observed actions

On the basis of our results, it is difficult to determine whether action verbs are associated with the same sensorimotor activity as observed actions. This is because of the different lateralization that we found for action verbs and observed actions. Action verbs were associated with left central activity, whereas observed actions were related to right central activity. The right central activity for the observed actions was stronger than the right central

as well as the left central activity for action verbs. Our findings are therefore similar to a study in adults, which reported stronger sensorimotor activity for observed actions than for action verbs (Moreno et al., 2013).

Despite the different lateralization for the two conditions, we found sensorimotor activity during both conditions. Our findings thus demonstrate that the sensorimotor system of 18- and 24-month-olds is involved in the processing of action verbs and observed actions. This provides evidence that the sensorimotor system is involved in the processing of different types of action representation early on in the process of verb acquisition. It further suggests a neural interrelation between action and language in toddlers, since our results showed that action and language share the sensorimotor system for their processing. Our findings extend the evidence for a language-action interrelation from behavioral and eye-tracking studies in toddlers, in which it was shown that toddlers anticipate action goals faster if they are presented with the verb beforehand compared to no verb presentation (Gampe & Daum, 2014). Furthermore, a study linking eye-tracking and transcranial magnetic stimulation (TMS) measures suggested that anticipatory gaze shifts, as measured in Gampe and Daum (2014), are associated with the suppression of the mu rhythm in adults (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013). The current study corroborates the evidence from these two studies that the interrelation of action and language is characterized by the involvement of the sensorimotor system in the processing of both domains of action representation.

4.2 Is the suppression of the mu rhythm different in response to action verbs than to pseudoverbs?

Similar to previous research with adults (Buccino et al., 2005; Fargier et al., 2012; Moreno et al., 2013; Repetto et al., 2013), our results revealed a distinct sensorimotor activation in

response to action verbs compared to other types of verbs. More specifically, our results showed that 18- and 24-month-olds activate their sensorimotor system during the processing of action verbs. For pseudoverbs, the sensorimotor system is just as involved as in the baseline (“I”). Most studies in adults used abstract verbs such as “to think” to contrast action verbs (Buccino et al., 2005; Moreno et al., 2013; Repetto et al., 2013), which is different from the contrast with pseudoverbs that we used. However, one study with adult participants indicated that the sensorimotor system was only involved in the processing of pseudoverbs after an associative training in which pseudoverb-action associations were formed (Fargier et al., 2012). This fits our results, which indicate that pseudoverb processing did not involve sensorimotor activity. This seems feasible, since the pseudoverbs were completely unfamiliar and no training preceded the presentation. In the current study, the difference between the neural processing of action verbs and pseudoverbs was only evident in the left central cluster, where sensorimotor activity was present for action verbs but not for pseudoverbs. Again, this lateralization could be due to the processing of linguistic action representations or due to imagined action execution. Very importantly, the difference in activity between action verbs and pseudoverbs in the left central area speaks against the assumption that sensorimotor activity during verb processing is merely associated with heard vocalizations.

Further, our results indicate that both action verbs and pseudoverbs are associated with occipital activity. Importantly, occipital activity did not differ between the two conditions. As discussed above (in 4.1.2), this could be due to attentional or processing demands. There are two possible explanations for these occipital effects, which are equally pronounced in both action verbs and pseudoverbs. In the following, we first offer a more low-level interpretation of this result, followed by a more high-level one. First, we have to consider that our baseline, which served to calculate the ERD scores, contained a linguistic stimulus, namely the “I”. This stimulus, in contrast to the action verb or the pseudoverb, is monosyllabic. It is possible

that disyllabic stimuli as our action verbs (e.g., “schnii-de”) and pseudoverbs (e.g., “schraa-de”) require a higher amount of overall processing than monosyllabic stimuli (e.g., “Ich”), which could be associated with a decrease in occipital alpha during the second acoustically presented word (“cut”) compared to the first (“I”). Second, the action verbs and pseudoverbs were embedded in a sentence structure. The sentences always started with “I”, which was followed by the action verb or the pseudoverb. The “I” might have served as a cue creating expectancy that something important might follow within the sentence structure. This expectancy could be associated with allocation of attention.

In summary, our results show that the sensorimotor system reacts only to action verbs, which have a motor-related meaning, but not to pseudoverbs that are unfamiliar. This means that, similar to research in adults (Moreno et al., 2013; Rüschemeyer et al., 2007), our findings support the hypothesis that action verbs that are strongly motor-related involve sensorimotor processing.

4.3 Is the suppression of the mu rhythm in response to verbs different for 18- and 24-month-olds?

The third main question of the current study was whether 18- and 24-month-olds differ in terms of sensorimotor involvement during verb processing. Our results indicate that there is no difference in sensorimotor processing of action verbs between the two age groups. In the introduction, we proposed two factors that could influence whether the sensorimotor processing of verbs differs or not: Expressive verb repertoire and motor experience. Expressive verb repertoire was assumed to be different between the two age groups (Golinkoff & Hirsh-Pasek, 2008; Kauschke, 2012). The results from our parent questionnaire support this assumption. The 18-month-olds vocalized the action verbs we used in our paradigm significantly less often than the 24-month-olds. If the children’s expressive

vocabulary influences the sensorimotor processing of verbs, one would expect a differential sensorimotor processing of verbs in the two age groups, which was not the case in the present study. With respect to motor experience, the age groups tested in the present study were not expected to differ because we used very basic means-end actions. The results from the parent questionnaire support this assumption. Both age groups had enough opportunity for associative learning with respect to mapping particular verbs onto particular actions. Therefore, if motor experience were the factor that drives differences in sensorimotor processing of action verbs, we would not expect to find differences between the age groups. Indeed, our results indicated that the two age groups did not differ with respect to the involvement of the sensorimotor system during action-verb processing. Accordingly, expressive verb repertoire is probably not a main factor that influences the sensorimotor processing of verb at this young age. However, it is possible that the parent questionnaire we used was not comprehensive enough and a broader measure of overall expressive vocabulary would be associated with differences in sensorimotor verb processing between the age groups. In future studies, language status should be tested in greater detail because previous studies linked expressive vocabulary size to toddlers' prediction of the continuation of a heard sentence (Mani et al., 2016; Mani & Huettig, 2012).

Furthermore, we assumed that first-hand motor experience could be associated with the processing of verbs. In our study, both age groups were familiar with the actions we presented, as indicated by the caregivers. Also, both age groups processed the action verbs in a similar way, which fits the result that both age groups are equally familiar with the actions. However, as regards the language questionnaire, our measure of motor experience might not have been sensitive enough to detect possible differences. We only asked the caregivers to indicate whether or not the toddlers performed the actions during playtime. Future studies could include other measures of motor experience by including standardized action execution

1 trials for all toddlers, or perhaps a test battery to account for fine-motor skills. Furthermore,
2 motor experience could be experimentally manipulated in a verb-learning paradigm, which
3 would be especially interesting in terms of the associative learning hypothesis (Cooper et al.,
4 2013).

6 **4.4 Future considerations**

7 There are at least three issues that need further attention in future studies. Firstly, since there
8 were strong occipital effects for all conditions in the current study, future studies should
9 carefully include occipital electrode clusters in their analysis (Cuevas et al., 2014). Secondly,
10 there were lateralized central effects in the current study. This makes comparisons between
11 the processing of action verbs and observed actions very difficult. Future studies should
12 consider balancing the location of the means object during presentation, in order to obtain
13 bilateral sensorimotor activity for observed actions. Alternatively, the location of the means
14 object could be experimentally manipulated, which would provide information about the role
15 of the object location in sensorimotor processing of actions. Finally, future studies could
16 include more comprehensive measures of language status and motor experience in order to
17 investigate their role in sensorimotor action-verb processing. Also, a learning paradigm in
18 which pseudoverbs are linked to unfamiliar actions could be fruitful for studying the role of
19 the type of motor experience (first-hand, observational) on verb processing and the associated
20 sensorimotor involvement.

22 **5. Conclusion**

23 The present study showed that the sensorimotor system of toddlers is activated during the
24 processing of action-related verbs. As in adults, the sensorimotor involvement was distinct for
25 familiar action verbs compared to pseudoverbs in toddlers at 18 and 24 months of age. This
26 means that the sensorimotor system is already involved in the processing of action verbs at

the beginning of verb acquisition. The comparison with the processing of observed actions indicates that the sensorimotor system underlies both action-verb and action processing. This suggests that the two different types of action representation, linguistic and visual, are interrelated on the neural level, since they share the sensorimotor system as their common processing system.

Acknowledgements

This work was supported by a grant from the International Max Planck Research School LIFE. We thank Ira Kurthen for her technical support in the EEG lab and with programming, and Laura Maffongelli and Claudio Campus for their advice on data processing and analysis.

References

- Bache, C., Kopp, F., Springer, A., Stadler, W., Lindenberger, U., & Werkle-Bergner, M. (2015). Rhythmic neural activity indicates the contribution of attention and memory to the processing of occluded movements in 10-month-old infants. *International Journal of Psychophysiology*, 98(2), 201–212. <https://doi.org/10.1016/j.ijpsycho.2015.09.003>
- Baker, M. C. (2003). *Lexical Categories: Verbs, Nouns and Adjectives*. Cambridge University Press.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59(1), 617–645. <https://doi.org/10.1146/annurev.psych.59.103006.093639>
- Bates, E., Marchman, V., Thal, D., Fenson, L., Dale, P., Reznick, J. S., ... Hartung, J. (1994). Developmental and stylistic variation in the composition of early vocabulary. *Journal of Child Language*, 21(01), 85–123.
- Berchicci, M., Zhang, T., Romero, L., Peters, A., Annett, R., Teuscher, U., ... Comani, S. (2011). Development of mu rhythm in infants and preschool children.

- 1 *Developmental Neuroscience*, 33(2), 130–143.
- 2 <https://doi.org/10.1159/000329095>
- 3 Biro, S., & Leslie, A. M. (2007). Infants' perception of goal-directed actions: Development
- 4 through cue-based bootstrapping. *Developmental Science*, 10(3), 379–398.
- 5 <https://doi.org/10.1111/j.1467-7687.2006.00544.x>
- 6 Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening
- 7 to action-related sentences modulates the activity of the motor system: A
- 8 combined TMS and behavioral study. *Cognitive Brain Research*, 24(3), 355–363.
- 9 <https://doi.org/10.1016/j.cogbrainres.2005.02.020>
- 10 Cooper, R. P., Cook, R., Dickinson, A., & Heyes, C. M. (2013). Associative (not Hebbian)
- 11 learning and the mirror neuron system. *Neuroscience Letters*, 540, 28–36.
- 12 <https://doi.org/10.1016/j.neulet.2012.10.002>
- 13 Cuevas, K., Cannon, E. N., Yoo, K., & Fox, N. A. (2014). The infant EEG mu rhythm:
- 14 Methodological considerations and best practices. *Developmental Review*, 34(1),
- 15 26–43. <https://doi.org/10.1016/j.dr.2013.12.001>
- 16 Daum, M. M., Prinz, W., & Aschersleben, G. (2008). Encoding the goal of an object-
- 17 directed but uncompleted reaching action in 6- and 9-month-old infants.
- 18 *Developmental Science*, 11(4), 607–619. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2008.00705.x)
- 19 [7687.2008.00705.x](https://doi.org/10.1111/j.1467-7687.2008.00705.x)
- 20 Daum, M. M., Prinz, W., & Aschersleben, G. (2009). Means-end behavior in young infants:
- 21 The interplay of action perception and action production. *Infancy*, 14(6), 613–
- 22 640. <https://doi.org/10.1080/15250000903263965>
- 23 DeBoer, T., Scott, L. S., & Nelson, C. A. (2013). Methods for acquiring and analyzing infant
- 24 event-related potentials. In M. de Haan (Ed.), *Infant EEG and Event-Related*
- 25 *Potentials* (pp. 5–37). Psychology Press.

- 1 Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-
2 trial EEG dynamics including independent component analysis. *Journal of*
3 *Neuroscience Methods*, 134(1), 9–21.
4 <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- 5 Elsner, C., D’Ausilio, A., Gredebäck, G., Falck-Ytter, T., & Fadiga, L. (2013). The motor
6 cortex is causally related to predictive eye movements during action observation.
7 *Neuropsychologia*, 51(3), 488–492.
8 <https://doi.org/10.1016/j.neuropsychologia.2012.12.007>
- 9 Eriksson, M., Westerlund, M., & Berglund. (2002). A screening version of the Swedish
10 Communicative Development Inventories designed for use with 18-month-old
11 children. *Journal of Speech, Language & Hearing Research*, 45(5), 948–960.
12 [https://doi.org/10.1044/1092-4388\(2002/077\)](https://doi.org/10.1044/1092-4388(2002/077))
- 13 Fargier, R., Paulignan, Y., Boulenger, V., Monaghan, P., Reboul, A., & Nazir, T. A. (2012).
14 Learning to associate novel words with motor actions: Language-induced motor
15 activity following short training. *Cortex*, 48(7), 888–899.
16 <https://doi.org/10.1016/j.cortex.2011.07.003>
- 17 Feldman, H. M., Dale, P. S., Campbell, T. F., Colborn, D. . K., Kurs-Lasky, M., Rockette, H. E.,
18 & Paradise, J. L. (2005). Concurrent and predictive validity of parent reports of
19 child language at ages 2 and 3 years. *Child Development*, 76(4), 856–868.
20 <https://doi.org/10.1111/j.1467-8624.2005.00882.x>
- 21 Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L.
22 (2016). Motor system activation predicts goal imitation in 7-month-old infants.
23 *Psychological Science*, 27(5), 675–684.
24 <https://doi.org/10.1177/0956797616632231>
- 25 Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the

- 1 motor system in language comprehension. *The Quarterly Journal of Experimental*
- 2 *Psychology*, 61(6), 825–850. <https://doi.org/10.1080/17470210701623605>
- 3 Friedrich, M., & Friederici, A. D. (2005). Phonotactic knowledge and lexical-semantic
- 4 processing in one-year-olds: Brain responses to words and nonsense words in
- 5 picture contexts. *Journal of Cognitive Neuroscience*, 17(11), 1785–1802.
- 6 <https://doi.org/10.1162/089892905774589172>
- 7 Gampe, A., Brauer, J., & Daum, M. M. (2016). Imitation is beneficial for verb learning in
- 8 toddlers. *European Journal of Developmental Psychology*, 13(5), 594–613.
- 9 <https://doi.org/10.1080/17405629.2016.1139495>
- 10 Gampe, A., & Daum, M. M. (2014). Productive verbs facilitate action prediction in
- 11 toddlers. *Infancy*, 19(3), 301–325. <https://doi.org/10.1111/infa.12047>
- 12 Ganea, P. A., & Saylor, M. M. (2013). Representational constraints on language
- 13 development: Thinking and learning about absent things. *Child Development*
- 14 *Perspectives*, 7(4), 227–231. <https://doi.org/10.1111/cdep.12045>
- 15 Ganea, P. A., Shutts, K., Spelke, E. S., & DeLoache, J. S. (2007). Thinking of things unseen:
- 16 Infants' use of language to update mental representations. *Psychological Science*,
- 17 18(8), 734–739. <https://doi.org/10.1111/j.1467-9280.2007.01968.x>
- 18 Gentner, D., & Boroditsky, L. (2001). Individuation, relativity, and early word learning. In
- 19 M. Bowerman & S. C. Levinson (Eds.), *Language acquisition and conceptual*
- 20 *development* (pp. 215–256). Cambridge, UK: Cambridge University Press.
- 21 Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not
- 22 observational training, alters neurocognitive mechanisms of action processing in
- 23 infancy. *Journal of Cognitive Neuroscience*, 27(6), 1207–1214.
- 24 https://doi.org/10.1162/jocn_a_00774
- 25 Golinkoff, R. M., & Hirsh-Pasek, K. (2006). Introduction: Progress on the verb learning

- front. In K. Hirsh-Pasek & R. M. Golinkoff (Eds.), *Action meets word. How children learn verbs* (pp. 3–28). New York: Oxford University Press.
- Golinkoff, R. M., & Hirsh-Pasek, K. (2008). How toddlers begin to learn verbs. *Trends in Cognitive Sciences*, 12(10), 397–403. <https://doi.org/10.1016/j.tics.2008.07.003>
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301–307. [https://doi.org/10.1016/S0896-6273\(03\)00838-9](https://doi.org/10.1016/S0896-6273(03)00838-9)
- Hauk, O., & Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience*, 5, 149. <https://doi.org/10.3389/fnhum.2011.00149>
- Hernandez Jarvis, L., Merriman, W. E., Barnett, M., Hanba, J., & van Haitsma, K. S. (2004). Input that contradicts young children’s strategy for mapping novel words affects their phonological and semantic interpretation of other novel Words. *Journal of Speech, Language, and Hearing Research*, 47(2), 392–406. [https://doi.org/10.1044/1092-4388\(2004/032\)](https://doi.org/10.1044/1092-4388(2004/032))
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience & Biobehavioral Reviews*, 34(4), 575–583. <https://doi.org/10.1016/j.neubiorev.2009.11.007>
- Hobson, H. M., & Bishop, D. V. M. (2016). Mu suppression – A good measure of the human mirror neuron system? *Cortex*, 82, 290–310. <https://doi.org/10.1016/j.cortex.2016.03.019>
- James, K. H., & Maouene, J. (2009). Auditory verb perception recruits motor systems in the developing brain: An fMRI investigation. *Developmental Science*, 12(6), F26–F34. <https://doi.org/10.1111/j.1467-7687.2009.00919.x>
- Jeon, Y., Nam, C. S., Kim, Y.-J., & Whang, M. C. (2011). Event-related (De)synchronization (ERD/ERS) during motor imagery tasks: Implications for brain–computer

- 1 interfaces. *International Journal of Industrial Ergonomics*, 41(5), 428–436.
- 2 <https://doi.org/10.1016/j.ergon.2011.03.005>
- 3 Kauschke, C. (2012). *Kindlicher Spracherwerb im Deutschen*. Berlin: De Gruyter.
- 4 Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., ... Henningsen, H.
- 5 (2000). Handedness and hemispheric language dominance in healthy humans.
- 6 *Brain*, 123(12), 2512–2518. <https://doi.org/10.1093/brain/123.12.2512>
- 7 Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002).
- 8 Hearing sounds, understanding actions: Action representation in mirror neurons.
- 9 *Science*, 297(5582), 846–848. <https://doi.org/10.1126/science.1070311>
- 10 Locatelli, M., Gatti, R., & Tettamanti, M. (2012). Training of manual actions improves
- 11 language understanding of semantically related action sentences. *Frontiers in*
- 12 *Psychology*, 3. <https://doi.org/10.3389/fpsyg.2012.00547>
- 13 Luo, Y., & Johnson, S. C. (2009). Recognizing the role of perception in action at 6 months.
- 14 *Developmental Science*, 12(1), 142–149. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2008.00741.x)
- 15 [7687.2008.00741.x](https://doi.org/10.1111/j.1467-7687.2008.00741.x)
- 16 Mani, N., Daum, M. M., & Huettig, F. (2016). “Proactive” in many ways: Developmental
- 17 evidence for a dynamic pluralistic approach to prediction. *The Quarterly Journal*
- 18 *of Experimental Psychology*, 69(11), 2189–2201.
- 19 <https://doi.org/10.1080/17470218.2015.1111395>
- 20 Mani, N., Durrant, S., & Floccia, C. (2012). Activation of phonological and semantic codes
- 21 in toddlers. *Journal of Memory and Language*, 66(4), 612–622.
- 22 <https://doi.org/10.1016/j.jml.2012.03.003>
- 23 Mani, N., & Huettig, F. (2012). Prediction during language processing is a piece of cake—
- 24 But only for skilled producers. *Journal of Experimental Psychology: Human*
- 25 *Perception and Performance*, 38(4), 843–847. <https://doi.org/10.1037/a0029284>

- 1 Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months
2 to 4 years of age. *Clinical Neurophysiology: Official Journal of the International*
3 *Federation of Clinical Neurophysiology*, 113(8), 1199–1208.
4 [https://doi.org/10.1016/S1388-2457\(02\)00163-3](https://doi.org/10.1016/S1388-2457(02)00163-3)
- 5 Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu
6 rhythm in human infancy. *Developmental Cognitive Neuroscience*, 1(2), 110–123.
7 <https://doi.org/10.1016/j.dcn.2010.09.001>
- 8 Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation
9 and execution in 14-month-old infants: An event-related EEG desynchronization
10 study. *Developmental Science*, 14(3), 474–480. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2010.00991.x)
11 [7687.2010.00991.x](https://doi.org/10.1111/j.1467-7687.2010.00991.x)
- 12 McGarry, L. M., Russo, F. A., Schalles, M. D., & Pineda, J. A. (2012). Audio-visual
13 facilitation of the mu rhythm. *Experimental Brain Research*, 218(4), 527–538.
14 <https://doi.org/10.1007/s00221-012-3046-3>
- 15 McManus, I. C., & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance,
16 and lateralization. *Handbook of Neuropsychology*, 6, 115–115.
- 17 Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain
18 responses for action-words characterizes the link between language and action.
19 *Cortex*, 74, 262–276. <https://doi.org/10.1016/j.cortex.2015.10.021>
- 20 Moreno, I., de Vega, M., & León, I. (2013). Understanding action language modulates
21 oscillatory mu and beta rhythms in the same way as observing actions. *Brain and*
22 *Cognition*, 82(3), 236–242. <https://doi.org/10.1016/j.bandc.2013.04.010>
- 23 Munakata, Y. (2001). Graded representations in behavioral dissociations. *Trends in*
24 *Cognitive Sciences*, 5(7), 309–315. [https://doi.org/10.1016/S1364-](https://doi.org/10.1016/S1364-6613(00)01682-X)
25 [6613\(00\)01682-X](https://doi.org/10.1016/S1364-6613(00)01682-X)

- 1 Munakata, Y., McClelland, J. L., Johnson, M. H., & Siegler, R. S. (1997). Rethinking infant
2 knowledge: Toward an adaptive process account of successes and failures in
3 object permanence tasks. *Psychological Review*, 104(4), 686–713.
4 <https://doi.org/10.1037/0033-295X.104.4.686>
- 5 Nam, C. S., Jeon, Y., Kim, Y.-J., Lee, I., & Park, K. (2011). Movement imagery-related
6 lateralization of event-related (de)synchronization (ERD/ERS): Motor-imagery
7 duration effects. *Clinical Neurophysiology*, 122(3), 567–577.
8 <https://doi.org/10.1016/j.clinph.2010.08.002>
- 9 Nyström, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm
10 desynchronization to measure mirror neuron activity in infants: Measuring
11 mirror neuron activity in infants. *Developmental Science*, 14(2), 327–335.
12 <https://doi.org/10.1111/j.1467-7687.2010.00979.x>
- 13 Paulus, M., Hunnius, S., & Bekkering, H. (2013). Neurocognitive mechanisms underlying
14 social learning in infancy: Infants' neural processing of the effects of others'
15 actions. *Social Cognitive and Affective Neuroscience*, 8(7), 774–779.
16 <https://doi.org/10.1093/scan/nss065>
- 17 Paulus, M., Hunnius, S., van Elk, M., & Bekkering, H. (2012). How learning to shake a
18 rattle affects 8-month-old infants' perception of the rattle's sound:
19 Electrophysiological evidence for action-effect binding in infancy. *Developmental*
20 *Cognitive Neuroscience*, 2(1), 90–96. <https://doi.org/10.1016/j.dcn.2011.05.006>
- 21 Pfurtscheller, G. (2001). Functional brain imaging based on ERD/ERS. *Vision Research*,
22 41(10–11), 1257–1260. [https://doi.org/10.1016/S0042-6989\(00\)00235-2](https://doi.org/10.1016/S0042-6989(00)00235-2)
- 23 Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm
24 (de)synchronization and EEG single-trial classification of different motor imagery
25 tasks. *NeuroImage*, 31(1), 153–159.

- 1 <https://doi.org/10.1016/j.neuroimage.2005.12.003>
- 2 Pineda, J. A., Allison, B. Z., & Vankov, A. (2000). The effects of self-movement,
- 3 observation, and imagination on mu; rhythms and readiness potentials (RP's):
- 4 toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation*
- 5 *Engineering*, 8(2), 219–222. <https://doi.org/10.1109/86.847822>
- 6 Pineda, J. A., Grichanik, M., Williams, V., Trieu, M., Chang, H., & Keysers, C. (2013). EEG
- 7 sensorimotor correlates of translating sounds into actions. *Frontiers in*
- 8 *Neuroscience*, 7, 203. <https://doi.org/10.3389/fnins.2013.00203>
- 9 Pulverman, R., Hirsh-Pasek, K., Golinkoff, R. M., Pruden, S., & Salkind, S. (2006).
- 10 Conceptual foundations for verb learning: Celebrating the event. In K. Hirsh-
- 11 Pasek & R. M. Golinkoff (Eds.), *Action meets word: How children learn verbs* (pp.
- 12 134–159). New York: Oxford University Press.
- 13 Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews*
- 14 *Neuroscience*, 6(7), 576–582. <https://doi.org/10.1038/nrn1706>
- 15 Reid, V. M., Striano, T., & Iacoboni, M. (2011). Neural correlates of dyadic interaction
- 16 during infancy. *Developmental Cognitive Neuroscience*, 1(2), 124–130.
- 17 <https://doi.org/10.1016/j.dcn.2011.01.001>
- 18 Repetto, C., Colombo, B., Cipresso, P., & Riva, G. (2013). The effects of rTMS over the
- 19 primary motor cortex: The link between action and language. *Neuropsychologia*,
- 20 51(1), 8–13. <https://doi.org/10.1016/j.neuropsychologia.2012.11.001>
- 21 Rothweiler, M., & Kauschke, C. (2007). Lexikalischer Erwerb. In H. Schöler & A. Welling
- 22 (Eds.), *Sonderpädagogik der Sprache* (Vol. 1, pp. 42–56). Göttingen: Hogrefe
- 23 Verlag.
- 24 Rüschemeyer, S.-A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending:
- 25 Neural correlates of processing verbs with motor stems. *Journal of Cognitive*

- 1 *Neuroscience*, 19(5), 855–865.
- 2 Shinskey, J. L., & Munakata, Y. (2005). Familiarity breeds searching: Infants reverse their
- 3 novelty preferences when reaching for hidden objects. *Psychological Science*,
- 4 16(8), 596–600. <https://doi.org/10.1111/j.1467-9280.2005.01581.x>
- 5 Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the
- 6 newborn baby. *Proceedings of the National Academy of Sciences*, 105(2), 809–813.
- 7 <https://doi.org/10.1073/pnas.0707021105>
- 8 Sootsman Buress, J., Woodward, A. L., & Brune, C. W. (2006). The roots of verbs in
- 9 prelinguistic action knowledge. In K. Hirsh-Pasek & R. M. Golinkoff (Eds.), *Action*
- 10 *meets word. How children learn verbs* (pp. 208–227). New York: Oxford University
- 11 Press.
- 12 Southgate, V., Johnson, M. H., Karoui, I. E., & Csibra, G. (2010). Motor System Activation
- 13 Reveals Infants' On-Line Prediction of Others' Goals. *Psychological Science*, 21(3),
- 14 355–359. <https://doi.org/10.1177/0956797610362058>
- 15 Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor
- 16 activation during action observation in human infants. *Biology Letters*,
- 17 rsbl20090474. <https://doi.org/10.1098/rsbl.2009.0474>
- 18 Springer, A., Huttenlocher, A., & Prinz, W. (2012). Language-induced modulation during
- 19 the prediction of others' actions. *Psychological Research*, 76(4), 456–466.
- 20 <https://doi.org/10.1007/s00426-012-0411-6>
- 21 Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during
- 22 observation of unusual versus ordinary actions in infancy. *Social Neuroscience*,
- 23 5(5–6), 451–460. <https://doi.org/10.1080/17470919.2010.490667>
- 24 Stroganova, T. A., Orekhova, E. V., & Posikera, I. N. (1999). EEG alpha rhythm in infants.
- 25 *Clinical Neurophysiology*, 110(6), 997–1012. <https://doi.org/10.1016/S1388->

- 1 2457(98)00009-1
- 2 Szagun, G., Stumper, B., & Schramm, S. A. (2009). *Fragebogen zur frühkindlichen*
- 3 *Sprachentwicklung (FRAKIS)*. Frankfurt am Main: Pearson Assessment &
- 4 Information GmbH.
- 5 Tomasello, M. (1992). *First verbs: A case study of early grammatical development*. New
- 6 York: Cambridge University Press.
- 7 Tomasello, M. (2001). Perceiving intentions and learning words in the second year of
- 8 life. In M. Bowerman & S. C. Levinson (Eds.), *Language acquisition and conceptual*
- 9 *development* (pp. 132–158). Cambridge, UK: Cambridge University Press.
- 10 Tomasello, M., & Mervis, C. B. (1994). The instrument Is great, but measuring
- 11 comprehension is still a problem. *Monographs of the Society for Research in Child*
- 12 *Development*, 59(5), 174–179. [https://doi.org/10.1111/j.1540-](https://doi.org/10.1111/j.1540-5834.1994.tb00186.x)
- 13 [5834.1994.tb00186.x](https://doi.org/10.1111/j.1540-5834.1994.tb00186.x)
- 14 van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never
- 15 crawl alone: Neurophysiological evidence for experience-dependent motor
- 16 resonance in infancy. *NeuroImage*, 43(4), 808–814.
- 17 <https://doi.org/10.1016/j.neuroimage.2008.07.057>
- 18 van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of
- 19 motor activation in language processing: Motor cortical oscillations support
- 20 lexical-semantic retrieval. *NeuroImage*, 50(2), 665–677.
- 21 <https://doi.org/10.1016/j.neuroimage.2009.12.123>
- 22 Warreyn, P., Ruyschaert, L., Wiersema, J. R., Handl, A., Pattyn, G., & Roeyers, H. (2013).
- 23 Infants' mu suppression during the observation of real and mimicked goal-
- 24 directed actions. *Developmental Science*, 16(2), 173–185.
- 25 <https://doi.org/10.1111/desc.12014>

- 1 Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach.
2 *Cognition*, 69(1), 1–34. [https://doi.org/10.1016/S0010-0277\(98\)00058-4](https://doi.org/10.1016/S0010-0277(98)00058-4)
3 Yoo, K. H., Cannon, E. N., Thorpe, S. G., & Fox, N. A. (2016). Desynchronization in EEG
4 during perception of means-end actions and relations with infants' grasping skill.
5 *British Journal of Developmental Psychology*, 34(1), 24–37.
6 <https://doi.org/10.1111/bjdp.12115>

7